

THE SALT GLAND OF THE HERRING GULL¹

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The long known fact that the nasal gland is conspicuously larger in marine birds than in terrestrial species has recently been given a functional explanation. It has been found that in birds taking their food from the ocean the nasal gland is developed into an organ whose main function is the secretion of salt. We have, therefore, in our publications on the function of this gland, referred to it as the "salt gland." After large salt intake, due to ingestion of sea water or marine invertebrate organisms, the salt gland assists the kidney in the excretion of excess of sodium chloride. In some marine birds the gland is more important than the kidney in the elimination of salt from the organism (Schmidt-Nielsen and Sladen, 1958; Schmidt-Nielsen and Fänge, 1958b).

The anatomy of the avian nasal gland in a large number of birds, both terrestrial and marine, was described in a monograph by Technau (1936). Although Technau mainly dealt with the gross anatomy of the gland he also made histological observations. Other microscopical observations have been made by Marples (1932) and Mihalik (1932), and the embryology has been studied by Grewe (1951).

The discovery of the osmoregulatory importance of the salt gland of marine birds made it necessary to re-investigate its histology in the light of the present knowledge of its function.

MATERIALS AND METHODS

The material consisted of young specimens of the herring gull (*Larus argentatus*) caught at the Atlantic coast at Beaufort, North Carolina, and at Mount Desert Island, Maine.

For histological examination glands were fixed in Bouin's fluid, and paraffin sections were stained in azan (Romeis, 1924) or haematoxylin-eosin.

The main structure of the arterial supply to the gland was studied by injection of methacrylate plastic into the carotid arteries, followed by maceration of the tissues with KOH. The detailed vascularization was studied in preparations injected with India ink through the carotids, fixed in Bouin's fluid, and subsequently cleared in benzyl benzoate. The glandular duct system was studied by injection of India ink or methacrylate plastic into the lateral duct opening. Paraffin sections were prepared of some of the India ink-injected specimens.

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Gross anatomy

In the gull the large, paired salt gland is situated on the top of the skull in the supraorbital grooves of the frontal bone (Fig. 1). Strictly speaking each gland consists of two parts, as seen from the fact that there are two ducts on each side of the head leading forwards into the beak (Technau, 1936). However, the two parts of the gland have a similar structure and are joined so closely together that they can be considered as one functional unit and may be regarded as one gland. Thus, the glands are flat and crescent shaped, and two ducts pass from the anterior end of each to the anterior nasal cavity (vestibulum). On the upper side the gland is covered by a thin, tough connective tissue membrane. The anterior part of it extends somewhat laterally from the margin of the frontal bone and forms part of the roof of the orbit. Blood vessels and nerves pass from the orbit into the gland through holes in the frontal bone.

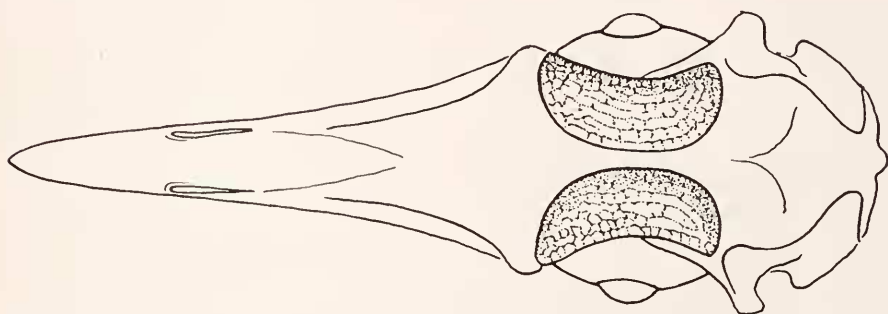


FIGURE 1. Skull of the herring gull from above, showing the position of the salt gland.

The two ducts on each side of the head take their origin from the lower side of the anterior part of the gland and run close together into the beak, where they open at the posterior end of the vestibular concha (Marples, 1932; Technau 1936). The lateral duct opens on the lower median side of the vestibular concha (pre-concha) while the median duct has its opening on the nasal septum close to the transverse fold separating the anterior nasal cavity (vestibulum) from the upper nasal cavity. The openings of the ducts can be found if a longitudinal incision is made in the palate somewhat lateral to the midline, and it is then possible to cannulate the lateral duct opening for the collection of secretion in living birds (Fänge, Schmidt-Nielsen and Robinson, 1958), or for injection of fluids into the duct. For some reason our attempts to cannulate the median duct were unsuccessful.

Marples (1932) found in *Larus ridibundus* (black-headed gull) that the ducts are formed at an early embryonic stage as outgrowths from the nasal cavity. Later the ducts branch above the frontal bone, forming the glandular tissue. Corresponding to the branches of the embryonic ducts, the gland of the adult is composed of tubes or lobes, giving it a characteristic surface structure (Fig. 2). Most of the gland consists of long lobes, some of which stretch along the whole length of the gland. In the gland of *Larus argentatus* about 15 such longitudinal

lobes can be seen in a transversal section. In addition to these longitudinal lobes there are shorter lobes oriented in various directions.

In our material the combined weight of the two salt glands varied from 700 to 900 mg. The weight of the animals was 700–1000 grams (young specimens). Technau (1936) found in the herring gull a gland weight (probably unilateral), of 555 mg., but in the related common gull, *L. canus*, 150 mg., and in the black-headed gull, *L. ridibundus*, only 50 mg. Of these three gulls, the herring gull is the most salt water-bound species while the black-headed gull is, to a large extent, associated with fresh water. Thus, there is a good correlation between the size of the salt gland and the habitat of the different gull species (Schildmacher, 1932).

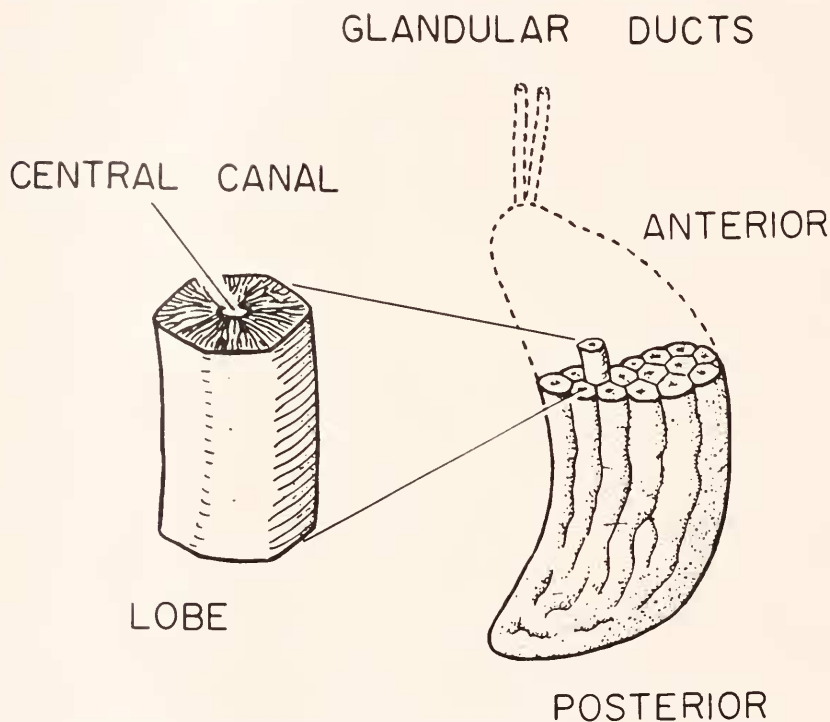


FIGURE 2. Diagram showing the gross structure of the salt gland (left side).

Microscopic structure

In each lobe there is a central canal (Fig. 2) which connects with the lumen of one of the two main ducts from the gland. Branching tubular glands radiate out from this central canal which is surrounded by a rather voluminous connective tissue mass (Figs. 3, 4). Close to the central canal, where the gland tubules have not yet branched extensively, the tubules are round in transverse section and separated by the connective tissue. In the periphery of the lobe the tubules are closely packed together and run parallel to each other, separated by very delicate connective tissue membranes and blood capillaries. In tangential sections through

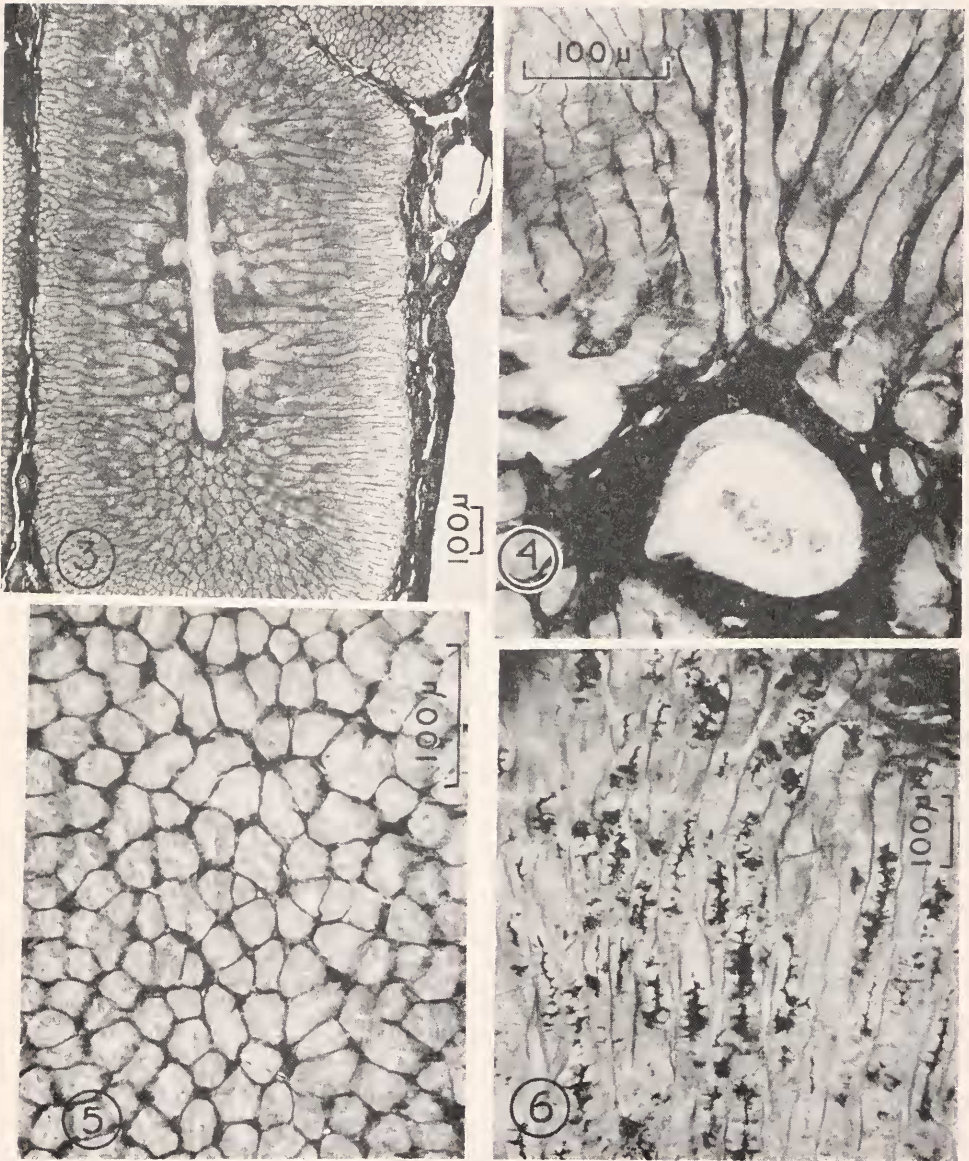


FIGURE 3. Longitudinal section through a lobe. Note the difference in stainability between the outer and the inner zone of tubules. The blue-stained connective tissue is dark, due to use of a yellow filter when taking the microphotograph. (Bouin's fluid, azan.)

FIGURE 4. Transverse section through the central part of a lobe. An artery (vertical in the figure) passes into the connective tissue around the central canal. (Bouin's fluid, azan, yellow filter.)

FIGURE 5. Tangential section through a lobe half-way between the surface of the lobe and the central canal. The capillaries between the tubules are partly filled with blood. (Bouin's fluid, azan, yellow filter.)

FIGURE 6. Transverse section through a lobe halfway between the surface and the central canal. India ink was injected into the lateral duct of the gland before fixation. (Bouin's fluid, azan.)

the peripheral parts of a lobe the cross-sectioned tubules have a polygonal outline and form a honeycomb-like pattern (Fig. 5).

The tubules branch 4–6 times forming different “generations” or “orders” of tubules. In the center of the lobe, close to the central canal, the tubules are thick and consist of cylindrical epithelial cells with the approximate dimensions $6\mu \times 15\text{--}20\mu$. In the periphery of the lobe the diameter of the tubules is smaller, and here the size of the cell is $6\text{--}9\mu \times 6\text{--}9\mu$. The cell nuclei are about the same size in

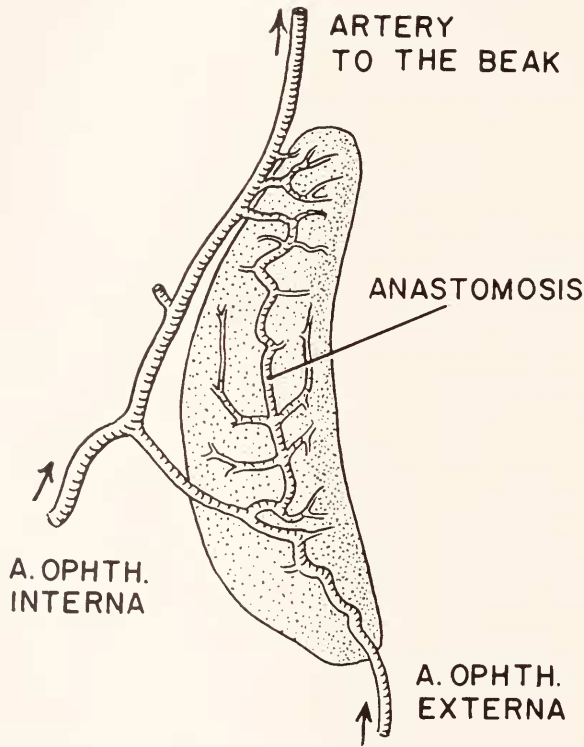


FIGURE 7. The arterial supply of the salt gland. The sketch shows the left gland from below. Drawn from a methacrylate plastic cast of the vascular system.

the central and the peripheral tubules. Thus, the amount of cytoplasm in relation to the nuclear volume is largest in the central portion of the tubules, possibly indicating that these gland cells carry out more work than those of the peripheral portions.

The cytoplasm of the cells has a lamellated or striated appearance. The striation is not limited to a striated border, but extends through the cells from the lumen to the periphery, where the cells are in contact with blood capillaries. In sections from specimens in which India ink had been injected into the lateral duct, the lumen of the tubules had an irregular shape, indicating the presence of secretory intra- or intercellular canaliculi (Fig. 6).

The cytoplasm takes a reddish colour in azan stain. In the most peripheral part of the tubules the cytoplasm is less heavily stained than in the central tubules (Fig. 3).

The central canal consists of 2-4 layers of cuboidal epithelium. The two main ducts passing to the anterior nasal cavity also consist of a multi-layered epithelium. In some preparations the boundaries between the epithelial cells, especially those of the central canal, had a vacuolated appearance which gave the illusion of a system of intercellular canals. This, however, could be a fixation artefact due to shrinkage of the cells. The two main ducts are surrounded by the same connective tissue which surrounds the accompanying blood vessels and nerve and have no connective tissue of their own. No smooth muscle cells could be found in the walls of the ducts. Neither was it possible to detect any smooth muscle in the gland except that of the arteries supplying the lobes. Neither the connective tissue of the upper side of the gland, the interlobular connective tissue mass, the connective tissue membranes around the tubules, nor the central connective tissue mass around the central canal contains any smooth muscle.

Vascularization

The blood supply of the nasal glands of the duck has been described by Marples (1932) and earlier authors (Gadow, 1891). According to our observations in *Larus argentatus* the main arterial supply comes from the arteria ophthalmica interna. The vessel penetrates the wall of the orbit above the optic nerve and, passing upwards along the median wall of the orbit, it divides into two branches to the salt gland. The anterior branch gives off several small arteries to the gland and then continues into the beak (Fig. 7). The posterior branch supplies the posterior part of the glands. Anastomosing with this branch another artery from the posterior wall of the orbit also gives blood to the gland. This artery probably corresponds to the arteria ophthalmica externa described by previous authors (Gadow, 1891; Slonaker, 1918). Both the arteria ophthalmica interna and the arteria ophthalmica externa are branches of the arteria carotis interna.

The arteries reaching the salt glands are among the largest arteries in the head of the gull. The arrangement of the arteries is such that, in spite of the rich blood supply, the blood could probably bypass the gland via the arterial arch formed by the anastomosis between the anterior and posterior branch of the arteria ophthalmica interna (Fig. 7). This arrangement may permit a large reduction in glandular blood flow without reducing the blood flow to the upper beak when the glands are not functioning. The control of the blood flow through the glands may be exerted by contractile arterioles in the glands.

The veins from the salt glands follow the arteries in their main courses (Marples, 1932).

Microscopic distribution of blood vessels

The connective tissue between the individual gland lobes contains a large number of branching arteries and veins. At intervals the arteries give off branches which pass into the lobes. These arteries pass straight through the gland tissue between the tubules towards the central canal without branching (Figs. 4, 8), but after reaching the central connective tissue mass they break up into numerous

capillaries. These capillaries, which have frequent branchings and anastomoses, run radially out towards the surface of the lobes. In their main course the capillaries are parallel to the tubules. Tubules and capillaries form a regular pattern in sections cut tangentially through a lobe (see Fig. 5). The tubules are polygonal in shape and the capillaries are situated at the corners of the polygons, each tubule being surrounded by 5–7 capillaries. The regularity of the arrangement reminds of the rete mirabile of the fish swimbladder, or the regular arrangement of tubules and blood vessels in the medulla of the mammalian kidney. At the surface of the

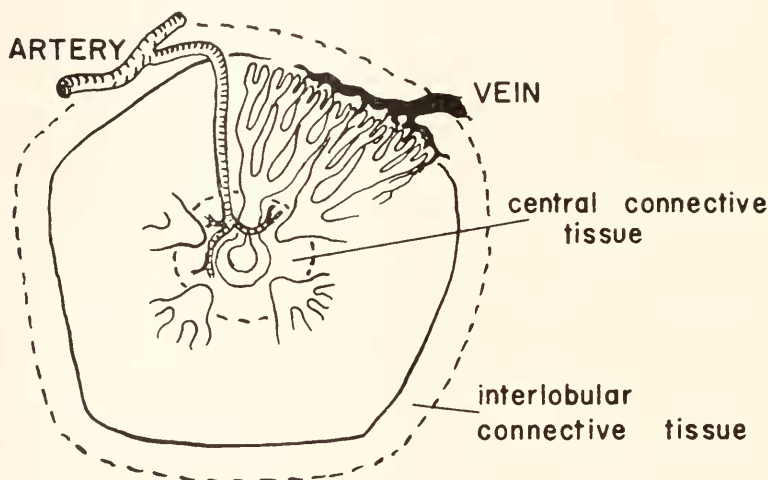


FIGURE 8. Diagram of a transverse section through a lobe of the salt gland.

lobe the capillaries leave the tubules and pass over into a venous plexus drained by veins in the interlobular connective tissue (Fig. 8). No veins were observed within the lobes. No lymph vessels could be observed in the glands, but as they may be difficult to detect in histological sections, we hesitate to claim that there are none in the salt gland. A diagrammatic picture of the blood flow in the gland is shown in Figure 9.

Innervation

The nasal gland of birds has been reported to be innervated from a parasympathetic ganglion in the anterior part of the orbit (Cords, 1904; Webb, 1957). The ganglion has connections with different cranial nerves and with the sympathetic system (Cords, 1904). The nerve supply of the salt gland in the herring gull will be described in another publication which will also deal with the physiological responses of the gland to various kinds of stimulation (Fänge, Schmidt-Nielsen and Robinson, 1958).

Other bird species

The presence of salt glands has been demonstrated in birds of five different orders (Schmidt-Nielsen and Fänge, 1958a). We have undertaken some pre-

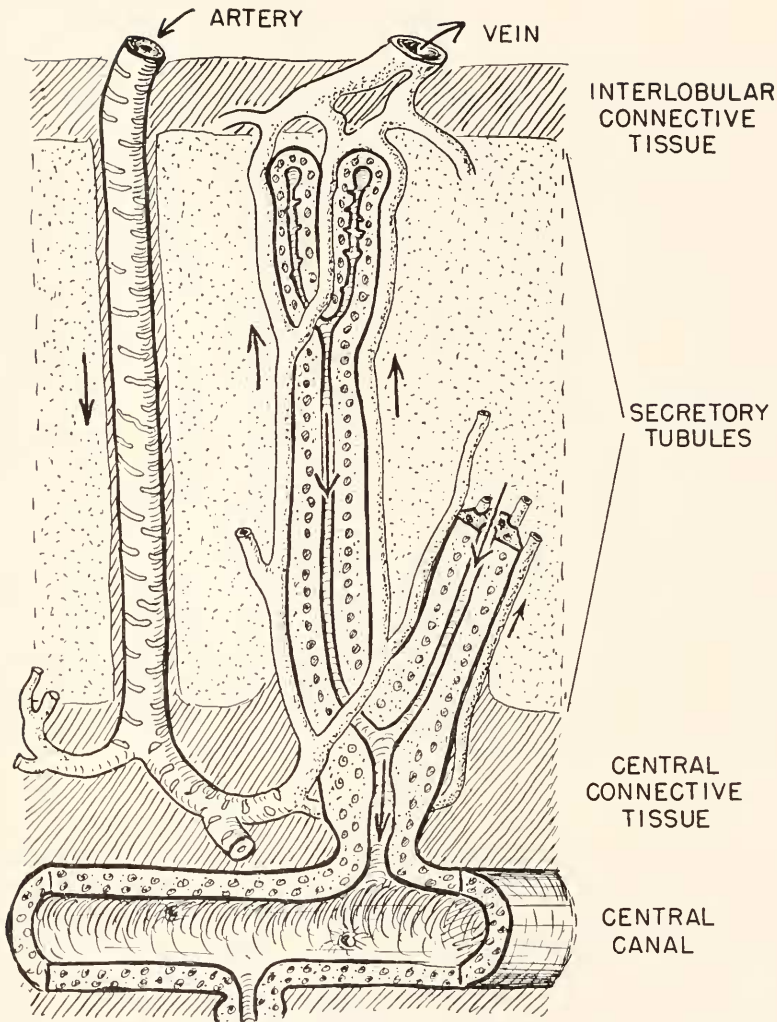


FIGURE 9. Diagram of the circulation showing the opposing directions of the flow in the gland tubules and in the capillaries. The tubules branch repeatedly, but for simplicity only two ramifications are pictured.

liminary histological studies of the salt glands of pelican (*Pelecanus*), cormorant (*Phalacrocorax*), eider duck (*Somateria*), petrel (*Oceanodroma*), etc. In these birds the glands have essentially the same histological structure as in the gull, and consists of lobes with tubular glands radially arranged around a central canal. In the pelican and the cormorant the lobes are not tubiform as in the gull, but rather short and of a rounded shape. In the connective tissue of the salt glands of many birds black pigment cells occur.

DISCUSSION

The salt gland of marine birds has a very characteristic structure consisting of closely packed secretory tubules with blood vessels between them. The tubules radiate from a central canal. In terrestrial birds, where the nasal glands have no salt excretory function, the glands contain only a few tubules or have sac-shaped diverticula instead of tubules (Marples, 1932). The strictly parallel arrangement of closely packed, glandular tubules may be necessary for the osmotic work performed by the gland. It is probable that the manner of distribution of the blood capillaries within the gland tissue is also of importance in this respect. It may be noted that the arrangement of blood vessels within the lobe is such that the capillary blood flows in a direction opposite to that of the secreted fluid. The functional significance of this counter-current flow in the salt gland is not clear. The counter-current principle, although manifested in a different way, seems to play an important role in the production of a concentrated urine in the kidney of mammals and birds (Hargitay and Kuhn, 1951). Although the structure of the salt gland in marine birds and of the mammalian kidney otherwise are entirely different, it is striking that a counter-current flow is found in both these organs, which in higher vertebrates are the only ones known to produce a highly hypertonic secretion.

The counter-current flow in the salt gland cannot, as such, explain the large osmotic work performed by the gland. Active ionic transport can be assumed to be the fundamental cellular process responsible for the osmotic work. The striated or lamellated appearance of the cytoplasm of the gland cells and the presence of secretory canaliculi indicate a highly specialized transport function of the cytoplasm. A more detailed study of the microscopic and electron microscopic structure of the cytoplasm of the avian salt gland cells is in progress.

SUMMARY

1. The salt gland of the herring gull (*Larus argentatus*) is a large, paired gland on top of the skull. On each side two ducts lead to the anterior nasal cavity. When the gland is secreting, its discharge comes out through the nares and drips off from the tip of the beak.

2. The gland has long, tubular lobes, each with a central canal. Tubulous glands radiate from the central canal. The gland cells have a striated or lamellated cytoplasm, and seem to have secretory canaliculi.

3. The blood supply is mainly from arteria ophthalmica interna. Within the gland the capillary blood flow is in a direction opposite to that of the secreted fluid. The innervation of the gland is from a ganglion of predominantly parasympathetic nature.

4. The salt glands of other marine birds have the same characteristic structure with the secreting tubules radiating out from a central canal.

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